

hystrix). I had never heard of this palm being reported so far north and west. Also wish to report successful growth of *Butia capitata* as far north as Montgomery, Alabama and in the Longview, Texas, area.

"Here in Colorado Springs I am having very good luck with *Erythea armata* and *E. edulis* as patio specimens. The two plants are three feet tall overall but growing vigorously at 6100 feet elevation. The dry air here seems to their liking. I will of course have to keep them indoors during the winters. These palms cause a lot of conversation as palms are very rare here.

"The palms photographed growing outdoors in Biloxi were: *Arecastrum Romanzoffianum*, *Washingtonia filifera*, *W. robusta*, *Phoenix canariensis*, *Sabal texana*, *S. Palmetto*, *Livistona chinensis*, *Butia capitata* and *Acoelorrhaphe (Paurotis) Wrightii*."

* * *

P.S. to the Seed Bank report above: If by chance you did not receive one of the form letters, enclosing the list of species available, please let me know so I can send one.

Also, fresh seeds of *Chrysalidocarpus Cabadae* will be coming along at intervals. If yours do not germinate, or you want more, kindly advise.

* * *

Invitations: Mr. H. M. Spencer-Lewin, of "Soncy", Point Shares, Bermuda, writes: "Please tell anyone who may be interested that my garden is open to any member who may be in Bermuda." And Mr. Ura Snidvongs, of Bangkok, Thailand, writes: "If any member of our Society will come to Thailand, please let me know; I will be pleased to bring him to my home and give any information he wants."

LUCITA H. WAIT

Translocation of Water and Nutrients In Palms

MARTIN H. ZIMMERMANN

The never-ending struggle of plants to reach a place in the sun led to the development of tall plants. A forest demonstrates this competition for light very clearly. Tall trees whose crowns are part of the general canopy — the forester calls them dominant trees — live under distinctly advantageous conditions when compared with shorter, so-called suppressed trees of the same species. It is not surprising then that the latter often succumb from lack of sufficient light. If we plant the same kind of tree in an open field, let us say in a meadow, in which it is artificially protected from competition because the meadow is regularly mowed and thus the growth of any other tall plant prevented, it does not grow as tall as its cousin in

the forest, but more bushy which is, under these conditions, a more effective way of capturing the maximum amount of light.

As a tree grows in height the distance over which water and nutrients must be transported internally increases. Two types of long-distance transport are involved. First, leaves have to be supplied with water and mineral nutrients from the soil. This is movement up the tree. The leaves are the places where organic foodstuffs (carbohydrates) are manufactured by photosynthesis. Other parts of the plant which are unable to carry out photosynthesis, or sufficient photosynthesis, like roots, stems, buds, flowers or fruits, have to be supplied with carbohydrates which are produced in

excess in the leaves. This second type of movement may be up or down the tree. It is clear, of course, that the longer the distances are the more energy has to be provided to maintain this transport. Under severe environmental conditions, for example in dry areas, less energy is available; plants cannot grow tall.

Channels of transport are very distinct in some trees and were recognized three hundred years ago by simple experiments. If a ring of bark is removed from a tree trunk (an operation called "girdling"), water still reaches the leaves (they do not wilt), but photosynthetic foodstuffs are prevented from passing the girdle and the roots are starved. This basic experiment as well as many more elaborate ones have taught us that water and minerals ascend from roots to leaves in the wood (the xylem) and photosynthetic nutrients are exported from leaves to places of need via the innermost layer of the bark (the phloem). This grand circulation system enables a land plant to distribute nutrients throughout its body in an effective manner.

Whoever has observed the growth of a tree has noticed that its stem grows in thickness as long as it lives. A growing layer between wood and bark, called the vascular cambium, produces regular layers of xylem toward the inside (the growth rings of the wood) and phloem to the outside. Thus, the vascular tissue is constantly renewed, and it is a well-known fact to botanists that all translocation takes place through relatively young tissue, in many cases less than one year old.

Let us now turn our attention to palms. The situation here is in many respects quite similar, but in other ways distinctly different [see also the article of Tomlinson (1961b) in this journal].

Palms do not increase the diameter of their stem once it is established; they just grow in height. In a population of palms of one species, the tallest individuals are usually the oldest. A young palm looks disproportionately stubby and an old, tall one disproportionately slender. Vascular tissues, once established in the stem, do not change but remain functional as translocation channels throughout the whole life of the palm. The functional permanence of these channels in a palm is therefore in sharp contrast to a tree like an oak or a pine where vascular tissues are regularly renewed. The arrangement of xylem and phloem in the stems of palms is also very different from that in a tree. Small strands of xylem and phloem are joined into units called vascular bundles which are distributed throughout the whole stem. Individual vascular bundles rarely exceed one millimeter ($1/25$ of an inch) in diameter and are usually much thinner. A great number of them run along the stem; in a small palm like *Rhapis* or *Chamaedorea* perhaps 1000 can be counted on a single transverse section, and in a large palm we may find as many as 50,000. Distribution and course of vascular bundles (the "plumbing system" of the palm) has been described in an earlier paper in this journal (Zimmermann & Tomlinson, 1965b) and in more technical detail elsewhere (Zimmermann & Tomlinson, 1965a).

Looking under microscopic magnification at a vascular bundle and the cellular matrix in which it is embedded, we can see four different types of tissues which are associated with the four major functions of the palm stem (Fig. 1 & 2; see also Figs. 70-72 in Zimmermann & Tomlinson, 1965b):

- (1) The fibrous bundle sheath which gives the stem its mechanical strength (F, Fig. 1). Vascular bun-

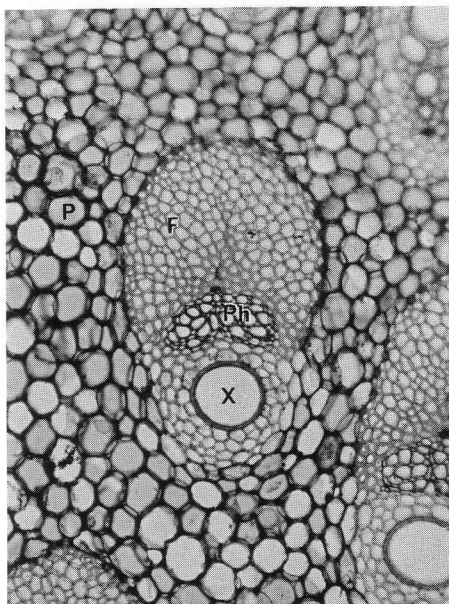


Fig. 1. A vascular bundle in the stem of *Rhaps excelsa* as seen in transverse section (100x). (F) the fibrous sheath of the bundle, giving the stem mechanical strength. (X) a xylem vessel, in which water ascends from roots to leaves. (Ph) the phloem; the larger cells are the sieve tubes where sugars move from leaves to other places. (P) the parenchyma, roundish cells of ground tissue in which surplus sugars are stored in the form of starch.

dles with greatly developed fibrous sheaths are crowded near the stem periphery where they are — from the engineering point of view — most effective in giving the stem mechanical support.

(2) One or more xylem vessels which serve as channels for water conduction (x). Vessels are capillaries formed by long series of dead cells. These barrel- or tube-like cells are lined up end to end and form continuous capillaries because their end walls are more or less broken through (Fig. 4).

(3) The phloem (Ph, Fig. 1) with its cell-series, the so-called sieve tubes, which serve as conducting channels for photosynthetic products. Sieve tubes are not merely tubes like the

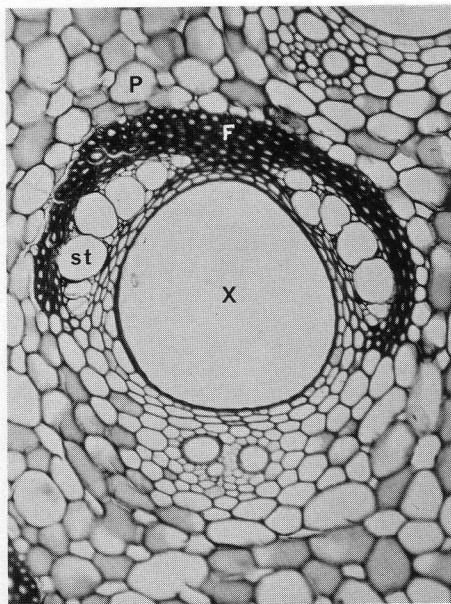


Fig. 2. A vascular bundle of a large-vessel palm (*Calamus*) at the same magnification (100x). Note that not only the xylem vessel (X) but also the sieve tubes (st) of the phloem are very large. The fibrous sheath (F) is not very strongly developed; the palm is a vine which does not support itself. (P) parenchyma.

vessels, they are living, highly specialized conducting cells (Figs. 5 and 6).

(4) The surrounding ground tissue (parenchyma, P) which represents the place where surplus carbohydrates are stored in the form of starch.

In plants with a vascular system like that of the palms where xylem and phloem are spatially very closely associated, translocation phenomena in the two different systems cannot be separated easily; the useful girdling experiments, for example, cannot be carried out. The few other experiments which have been made indicate that palms do not differ fundamentally from other plants. Let us review very briefly first the ascent of water and dissolved minerals in the xylem, then translocation

of organic nutrients in the phloem of palms.

The ascent of water and solutes in the xylem

Water may be "pulled" or "pushed" through vessels. Transpiration of water from the leaves pulls water up through the xylem of the stem. At the same time the roots may be pumping water into the xylem and thus raise the pressure above +1 atm. (atmospheric pressure) in the lower parts of the trunk (Davis, 1961). This pumping is a process consuming metabolic energy and is closely associated with the uptake of inorganic ions from the soil (Brower, 1965). But this root pressure alone is seldom sufficient to raise the water to the top of the palm when the leaves transpire vigorously on a sunny day, and it is quite clear that transpiration and the resulting pull in the xylem does most of the work. If a leaf or a part of a leaf is cut and dipped into a dye solution, the dye rapidly spreads into other leaves thus indicating pressures below +1 atm. in the xylem. Pressures may even drop below zero and become negative. Indeed, the palm *Calamus*, the rattan vine, is a classical example of a plant in which tensions (negative pressures) have been demonstrated experimentally (Scholander *et al.*, 1961). Water movement *per se* through the xylem is a purely physical phenomenon, taking place along a pressure gradient. During times of minimal transpiration, during a rainy night for example, the pressure gradient must be 0.1 atm./meter (i.e., that of a standing water column); during the height of transpiration on a sunny day, it is probably of the order of 0.15-0.2 atm./meter as it has been calculated for trees (Zimmermann, 1963, 1964). All available evidence indicates that the same phys-

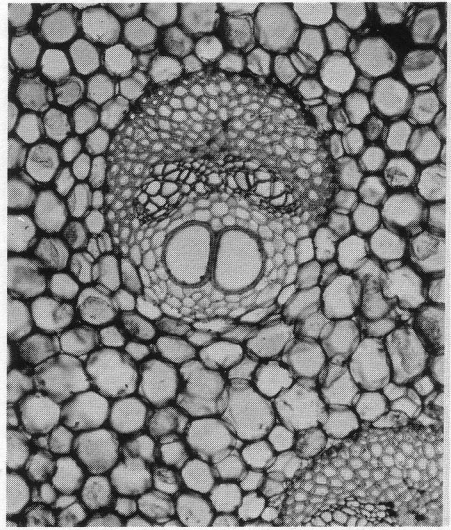


Fig. 3. A transverse section through a vascular bundle of *Rhapis excelsa* similar to that shown in Fig. 2 (100x). Two vessels overlap at this point. Water on its way up into the leaves has to move across the walls from one vessel to the other.

ical principles, known for trees, apply to palms.

Protection against injury and breakage of water columns in vessels is of paramount importance for the survival of plants. A ruptured vessel cannot continue to function because air is pulled into it when pressures are below atmospheric pressure and, *vice versa*, when pressures are above atmospheric it will leak. Vessels are by no means of infinite length, they are very short compared to the height of the palm. In *Rhapis excelsa*, for example, lengths of 10 cm (4 inches) have been measured. However, adjacent vessels overlap for an appreciable distance so that water can pass from one into the next through the permeable cell wall. Two such overlapping vessels are illustrated in Figure 3. When a vascular bundle is severed, the damage remains confined to the injured vessel because air cannot penetrate the tiny pores of a wet wall from one vessel to the next.

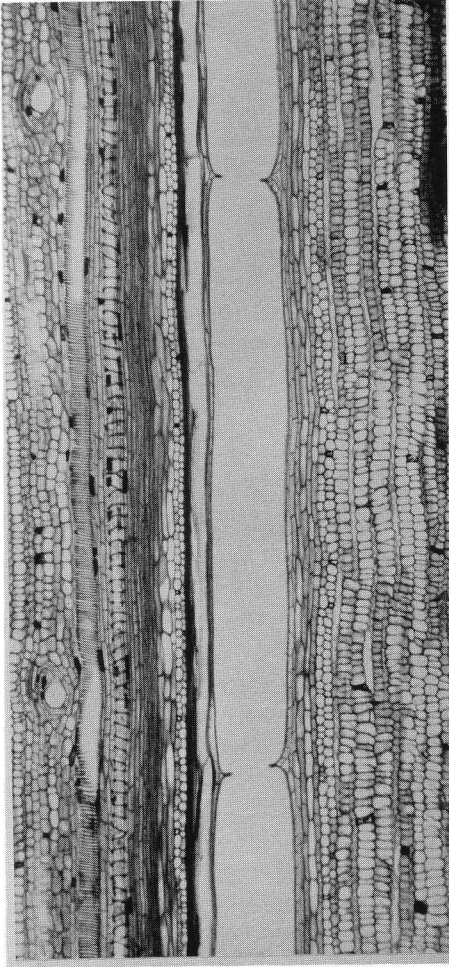


Fig. 4. A longitudinal section through a conducting bundle of *Calamus*, showing how vessels are made up of series of vessel elements, each the dead "shell" of an individual cell. The bottom and top walls are dissolved so that the cell series forms a capillary (i.e., the vessel). One whole vessel element can be seen in the center of the picture as well as part of the next above and the next below. Magnification 31½x.

Most palms have relatively small-diameter vessels; however, palms of the vine-type, such as the already mentioned *Calamus*, have very large-diameter vessels (Tomlinson, 1961a), and also very long vessels (Scholander *et al.*, 1961) (Fig. 2). Their water transport is much more efficient because of lower flow resist-

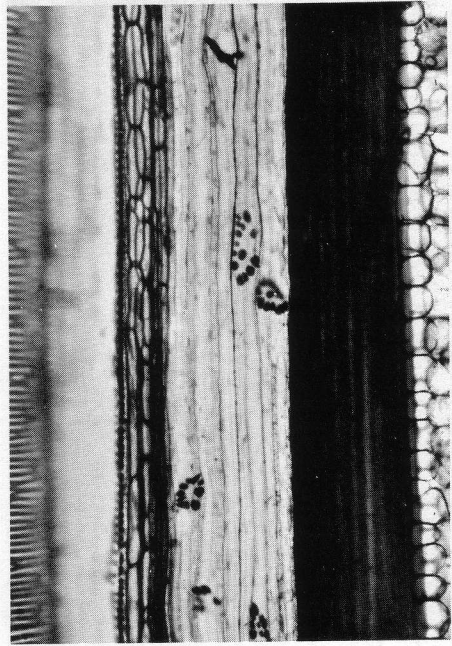


Fig. 5. Longitudinal section through a vascular bundle of the petiole of *Corypha umbraculifera* showing sieve tubes (the five series of long, light cells occupying about ¼ of the space in the center of the picture). The dark spots mark the end walls (sieve plates) between subsequent elements. The sieve plates are closed here by callose plugs, translocation could not take place. Magnification 88x. Photomicrograph by M. V. Parthasarathy.

ance, but it is obvious that such a system involves much greater risks in the event of injury. There are trees in temperate regions, the so-called ring-porous trees (most oaks for example), which have vessels of a similar size. These trees depend on an annual renewal of xylem for their survival (Huber, 1935; Zimmermann, 1963, 1964). There is no renewal of xylem in the palm stem, and we do not know how these highly specialized palms cope with the problem.

Transport of photosynthetic products in the phloem

Phloem transport is fundamentally different from xylem transport. Whereas the solute concentration in the xylem

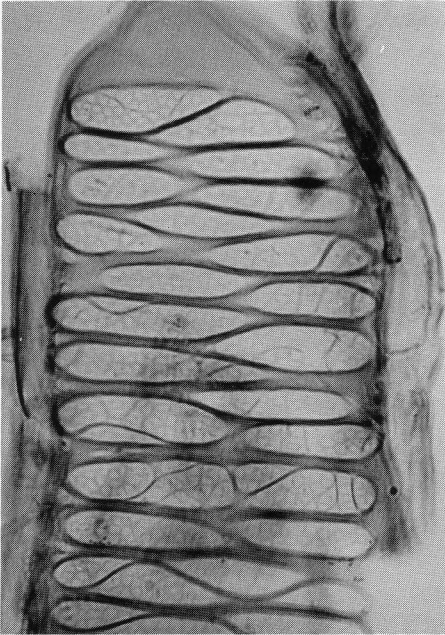
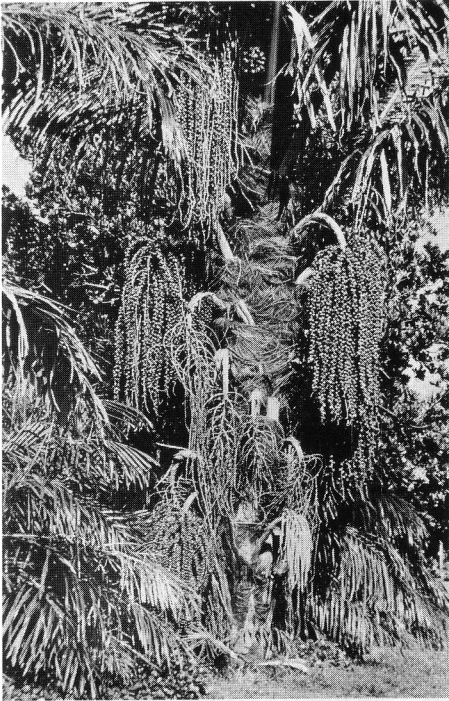


Fig. 6. View of an end wall (sieve plate) of a sieve element, a so-called sieve plate (*Borassus flabellifer*, root) The cell wall is perforated sieve-like, this is how the terms "sieve plate" and "sieve tube" originated. Magnification 490x. Photomicrograph by M. V. Parthasarathy.

is almost invariably extremely low (less than 0.5%), the concentration in the sieve tubes of the phloem is quite high (of the order of 10%, mostly sugars). Whereas water movement is largely a physical process, going along passively at low pressures through rigid, dead vessels, phloem transport depends intimately on the metabolic activity of living cells, proceeds through living sieve tubes, at high concentration and high positive pressures (Zimmermann, 1963, 1964). The mechanism of phloem transport is still vigorously debated by plant physiologists, but this is not the place to enter the argument. Let us relate, instead, some well-known phenomena in palms to our better knowledge of phloem transport in other plants. We can then see if our assumptions are reasonable.

The center of production of carbohydrates in palms is, of course, the crown of mature leaves. These export the bulk of their product (i.e., what they do not consume for their own respiration). Carbohydrates are needed in great quantities in the apex for the growth of young leaves which are not yet themselves photosynthesizing and for the further growth of the stem. Carbohydrates are also needed for the growth of inflorescences, and later for the developing fruits. All this requires fairly local transport at the very top of the palm. However, there is also considerable need for long-distance transport. The palm produces new roots continuously at the base of the stem so long as carbohydrates from leaves are available. Transport, therefore, must take place from leaves to roots. We know also that most palms store considerable amounts of starch in the ground tissue of their stems. It must be brought there via phloem. This storage material is of crucial importance in those palms which flower only during a short period at the end of their life span. Examples are *Corypha*, which produces a single terminal inflorescence (Fig. 9), and the *Caryotoideae*, which flower basipetally after completing their vegetative period of growth (Fig. 7). These palms translocate carbohydrates from mature leaves to the stem for storage as starch during their vegetative growth period. Then, during the reproductive phase, starch is mobilized and translocated into the inflorescence(s) within a relatively very short period of time.

In many parts of the tropics inflorescences of various species of palms are tapped and large quantities of sugary juice are obtained (Miller, 1964; see also the literature cited there). The juice is used locally as a source of sugar and for the manufacture of an alcoholic beverage, toddy. For *Arenga*,



7. Sugar palm, *Arenga pinnata*, at Fairchild Tropical Garden.

quantities up to 10 liters (over 2 gallons) per day are reported. A number of botanists have been interested in this phenomenon, but we owe most of our knowledge to a Dutchman, P. H. L. Tammes, who performed some very interesting experiments with exuding inflorescences (Tammes, 1933, 1952, 1958). The exudate contains about 15% solids, most of which is sugar (sucrose). Composition of the sap as well as all circumstantial evidence indicate that we are here dealing with an exudate from the phloem. Inflorescences which are cut from the stem continue to bleed for some time when put into water. It is also known that large quantities of starch are mobilized in the stem and translocated toward the inflorescence during the time of exudation because the starch content of the stem is depleted when the palm is tapped or when it flowers and sets fruit (Tammes, 1933).



8. Tapping the male inflorescence of *Arenga pinnata*. Note the short bamboo collecting tube. Photograph by Robert H. Miller. Reprinted from *Principes* 8:131. 1964.

This is exactly how the phloem behaves in most dicotyledonous trees. Cut ends of the sieve tubes are rapidly plugged and, when tapped, sugar in the sieve tubes is replenished from local reserve material. In dicotyledonous trees such an isolated sieve-tube system can be tapped with the mouth parts of an aphid (Weatherley *et. al.*, 1959). In the palm, flow is made possible by previous beating of the inflorescence, treatment which seems to slow down the clogging effect drastically. Even so, the cut end has to be sliced off at regular intervals to maintain the flow. It is not known precisely how the beating prevents clogging of the phloem.

In a further series of experiments, Tammes (1933) removed tapped inflorescences from the stem and put them with their cut end into solutions of various chemicals. He found that acid fuchsin (a red dye) was carried with the transpiration stream through the xylem to the (transpiring) flowers; the fuchsin could be detected in the xylem but neither in the phloem nor in the exudate. Ferrocyanide, however, was taken up into the phloem tissue; it was detected there as well as in the exudate



9. The appearance of the great flower cluster marks the gradual collapse of leaves on the stem of *Corypha umbraculifera*. Photograph by W. H. Hodge. Reprinted from *Principes* 5: 126. 1961.

by means of a simple histo-chemical reaction, the precipitation of Prussian blue with ferric chloride. This is perhaps the most elegant piece of evidence that sugar transport into the inflorescence takes place via phloem.

In conclusion we must admit that there are still many gaps in our understanding of translocation in palms. Palms have received far less attention from plant physiologists than they deserve, a neglect they share with many



10. At maturity, thousands of cherry-sized white fruits replace the cream-colored flowers of *Corpyha umbraculifera*. Photograph by W. H. Hodge. Reprinted from *Principes* 5: 127. 1961.

other tropical plants. We know that enormous quantities of water are daily lifted up to the leaves and considerable quantities of sugar are moved about the stem. This is an accomplishment few

people realize when they look at the quiet beauty of a palm.

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Palm Hunting Around the World

HAROLD E. MOORE, JR. *

VI. New Caledonia and Fiji

On Sunday, April 5th, after a morning of collecting and photographing *Metroxylon Warburgii* on the island of Efate, I finally boarded the plane for Noumea where M. Lucien Lavoix, a dedicated member of The Palm Society, met me. As we drove from the airport, M. Lavoix pointed out some of the vegetation types that were later to become familiar, and I noted that a *Veitchia* similar to that just collected on Efate was planted occasionally by houses along the road, as it is also in Noumea. After dinner and an introduction to M. Lavoix's wife and children, I unpacked my bags in the quarters of the South Pacific Commission near the herbarium of the Institut Francais d'Océanie where most of the plant drying was to be done. Thus began a whirlwind palm tour of New Caledonia.

April 6th was occupied partly with the inevitable processing of accumulated materials, partly with an afternoon trip to Mount Koghi where M. Lavoix has a home and garden set in the rain forest.

Here we looked at two kinds of *Basselinia*, a most perplexing genus which cannot, I think, be understood without considerable field work on the island. The one which we collected is one of the handsomest with solitary (though perhaps not always so) stems up to approximately 12 feet high, the trunk dark green or nearly black on new growth. The leaf sheath is also nearly black outside but when removed is glossy orange-yellow inside. Pinkish bracts of the inflorescence turn red-brown at anthesis splitting to expose the dark red-brown inflorescence crowded with tiny dark flowers. We were to see this palm and others very similar to it elsewhere. Other palms grow about M. Lavoix's home but these we left for another day in order to prepare for a journey to the north and east of the island.

Next morning a party consisting of M. Lavoix, M. Luc Chevalier of the Musée Calédonien, M. Robert Baret of the Forestry Department, myself, and Jacob Boulango as driver, set off in a well-loaded truck for the town of Koumac as the night's destination. At lunch-

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